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THE PHYLOGENY OF THE HYMENOPTERA.

By WILLIAM H. ASHMEAD.

You are all probably aware that the order Hymenoptera includes those insects known to us under the popular names of bees, wasps, hornets, ants, saw-flies, gall-flies, Ichneumons, and Chalcid-flies, and to-night I shall attempt to give you some idea of their origin, history, and development, their affinities with other orders, and their classification into groups, families, and tribes. I shall also attempt to show how the phytophagous species, under the great law of evolution, gave place to parasitic and predaceous species; and while I should like to mention some of the interesting and unsolved problems in their life-history, I shall be compelled, for want of time, to confine myself to the subject of my address and merely call your attention to the economic importance of the order.

A study of insects demonstrates that the same general laws of development that govern the higher animal life govern insect life and that there is ever an upward tendency to a higher or more specialized type; since man is the highest type of animal life, so a bee or an ant is the highest type of insect life.

Both in their way are remarkable productions of nature.

The surprising instincts and wonderful intelligence displayed by many Hymenoptera, particularly among the social species, in the construction of their habitations, in the care of their young and in gathering their food have been noticed and commented upon by many observers.

The late Prof. John O. Westwood as early as 1840 says: "If interesting habits and economy, great development of instinctive powers and social qualities be considered as indicating superiority in their possessors, the insects composing the order Hymenoptera have certainly far greater claims to be placed in the foremost ranks of insect tribes than any of their brethren."

Sir John Lubbock, known to us all for his researches in many departments of science, also says: "If we judge animals by their intelligence as evinced in their actions, it is not the gorilla and chimpanzee, but the bee and above all the ant, which approach nearest to man."

The Hymenoptera are also among the most useful and beneficial insects to man, since it is mostly only among the phytophagous species, or the saw-flies, horntails, etc., that we find those that are injurious; the vast majority of the species known to us being beneficial in various ways.

The hive-bee and other wild bees furnish us with wax and honey; while other bees are useful in the pollenization of plants and fruit trees, the legs of these insects, with their hairy covering, being specially adapted for carrying pollen from one flower to another. In fact, modern research has shown that many plants cannot be pollenized without the bees, and if it were not for these useful insects our orchards would be unproductive, since they are essential to the pollenization of the apple, the pear, the peach, and other fruit trees. It has also been shown that the bumble-bee is essential to the fertilization of red clover and other plants.

The oak-gall of commerce, the product of a cynipid, or gall-making wasp, has been for years utilized in the manufacture of ink, and, although to-day somewhat superseded by chemical products, is still much used in the manufacture of this important article of modern civilization.

The fig insects, the Agaonidæ or Blastophagæ, a most remarkable group of hymenopterous insects, belonging to the family Chalcididæ, are also important to man, since from time immemorial they have been made use of in the fertilization of the fig.

They are still made use of in the Orient, although it has been demonstrated that some varieties of figs—the artificial product of man through centuries of cultivation—will produce fruit without their intervention. All wild fig trees, however, are diœceous and it has been fully demonstrated that each species of fig tree has one or more species of these insects attached to it, which are essential to its fertilization.

All wasps—the wood-wasps, the digger-wasps, the social wasps, etc.—are also beneficial, and very few persons, outside of entomologists, can conceive of the immense services performed by these gayly-colored insects. All are predaceous or parasitic, and destroy annually thousands and thousands of destructive insect pests.

The economic value to us of the wasp and bee, however, is probably much less in comparison with the benefits we derive from innumerable parasitic ichneumon and chalcid flies. These are numbered by millions and are found everywhere. Most of them, too, are so minute or microscopic in size as to escape our notice, and it is only by the most careful observation in the field and by breeding in the laboratory that we are able to obtain a knowledge of their obscure mode of life.

These belong principally to five families, the Proctotrypidæ, Cynipidæ, Evaniidæ, Chalcididæ, Braconidæ, and Ichneumonidæ, and all of them except the gall-making cynipids and a few phytophagous chalcidids, are genuine parasites, living in and destroying the eggs, larvæ, pupæ, and imagoes of the destructive insect pests of the forest, field, and garden.

The obscure habits of these parasitic Hymenoptera are now being slowly worked out in various countries of the globe, and more particularly in Europe and America.

In recent years great interest in a study of these microscopic species has been manifested, and it is gratifying to us to know that in no country in the world is so much being done to make known the habits and economic value of these insects as in our own country. I allude particularly to the great work being done in the U. S. Department of Agriculture, by its field agents, and by our numerous Agricultural Experiment Stations.

Our knowledge of the habits of certain groups and genera of these insects is now sufficient to give us a good idea of those species which are most important to the agriculturist and fruit-grower.

For example, we have found out that whole groups of genera and species are parasitic in the eggs of other insects and that these are the most important.

The species belonging to the family Mymaridæ are parasitic in the eggs of Hemiptera, Diptera, Neuroptera, &c. Certain Proctotrypids belonging to the tribe Scelionini destroy the eggs of destructive orthopterous insects,—grasshoppers, katydids, locusts, &c.; the tribe Telenomini destroy lepidopterous, hemipterous, dipterous, and neuropterous eggs; the tribe Bæini, spider eggs; the tribe Teleasini, beetle eggs; while the family Trichogrammidæ destroy the eggs of moths, butterflies, beetles, bugs, &c. The species belonging to the genus Evania in the family Evaniidæ destroy the eggs of cockroaches; while some Chalcidids are also egg-destroyers, species of Encyrtus and Anastatus (= Antigaster).

The tribe Bethylini in the Proctotrypidæ are parasitic on the larvæ of the Micro-lepidoptera and on coleopterous larvæ; the subfamily Dryininæ on homopterous larvæ; the subfamily Platygasterinæ on dipterous larvæ; the subfamily Helorinæ on neuropterous insects; the subfamilies Proctotrypinæ and Belytinæ on coleopterous larvæ; while the Diapriinæ attack dipterous larvæ.

The parasitic Cynipidæ attack principally dipterous larvæ, although one subfamily, the Allotriinæ, destroy plant-lice belonging to the homopterous family Aphididæ.

The species belonging to the families Chalcididæ, Braconidæ, and Ichneumonidæ, comprising thousands and thousands of species, destroy the larvæ, pupæ, and imagoes of nearly all orders.

And we find in these families, just as we have found to be the case in the Proctotrypidæ, whole tribes and genera with a unity of habit that is universal. The genera Bracon, Spathius, Meteorus, Euphorus, Ichneumon, Pteromalus, Eupelmus, Aphelinus, Coccophagus, Tetrastichus, Melittobia, etc., have the same habits in Europe, Asia, Africa, or Australia as they have in America; and I hope to see the knowledge we are acquiring of these parasitic insects put to practical use.

I hope to live to see these parasites bred in great numbers in the laboratory and then transported into regions where they do not exist and where they will do the most good, in destroying their destructive insect hosts.

There is no reason why we cannot send our American parasites to other countries and receive in return other parasites not in our fauna.

Some of our most destructive insect pests were imported from foreign shores, and we should look to the original habitat of these insects for their natural enemies and parasites; and if these are not already with us, they should be imported.

The Phylogeny of Hexapous Insects.

From what I have said, I think I have clearly demonstrated the high rank of the order and its great economic importance, and will now proceed to show its phylogenetic developments and its position among other orders.

Dr. A. S. Packard, one of our best systematic entomologists, says: "There is nothing like a linear series in the animal kingdom, but it is like a tree. The higher series of orders form more of a linear series than the lower series, so that the Neuroptera, Orthoptera, Hemiptera, and Coleoptera form a more broken series than the Hymenoptera, Lepidoptera, and Diptera. A bee, butterfly, and house-fly are much more closely allied to each other than a beetle, squash-bug, a grasshopper, and a dragon-fly are among themselves."

This is quite true and a principle now almost universally accepted by zoologists.

Before proceeding with the phylogeny of the Hymenoptera, I shall, therefore, first attempt to show briefly the phylogeny of hexapodous insects, in an ideal genealogical tree.

This ideal tree is shown on my diagram No. 1.

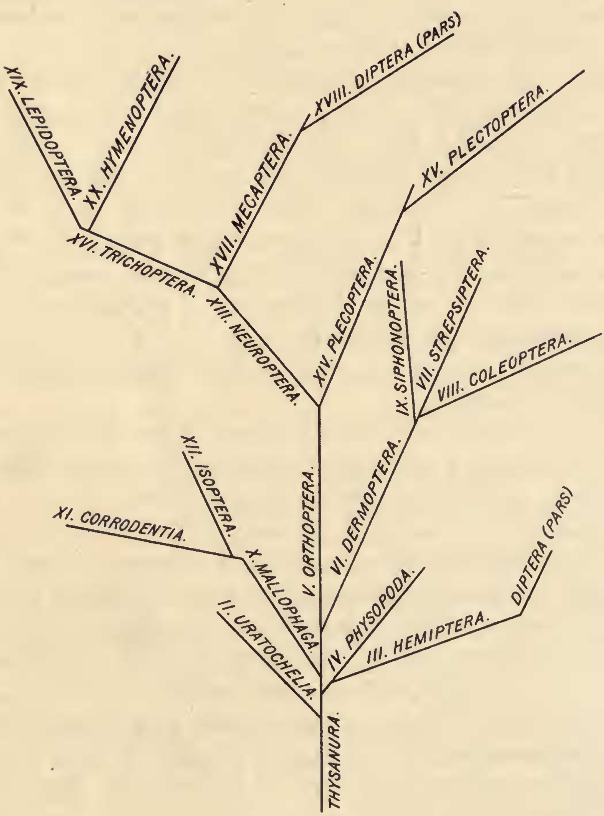
It will be observed that I agree with Brauer, Packard, Lubbock, and others in considering the order Thysanura as representing the less specialized type of insects and from which developed all others, which is emphasized again and again in the larval development of the different orders.

Twenty distinct orders are recognized, *Uratochelia* being a new order proposed for the family Japygidæ since I believe these insects, although closely allied, are quite distinct from other thysanurians.

This ideal genealogical tree will, I hope, enable you to at once grasp the affinities of the different orders and will show you the evolution that has taken place in their development.

It will also demonstrate to you more clearly than pages of

DIAGRAM No. 1.



Ideal Genealogical Tree of Insects.

text the evolution of insects from a primitive wingless type, without metamorphosis, into more specialized types of winged and wingless insects, with incomplete or complete metamorphosis.

The thysanurians, or springtails, are always apterous and undergo no distinct metamorphosis.

If in this ideal sketch of the phylogeny of insects I have drawn somewhat upon my imagination, instead of depending always upon facts, for my conception of their development, I have no apology to make; but, on the contrary, claim it is just as permissible for naturalists, as it is for philosophers to draw sometimes upon their imagination in order to interpret nature correctly.

This ideal genealogical tree is given merely to illustrate the origin of the Hymenoptera, and the position which I believe these insects should occupy among other orders, and I will now proceed to say something about this order.

The geological history of the Hymenoptera is very meagre. Some authorities, and especially Mr. Samuel H. Scudder, of Cambridge, Mass., our highest authority on fossil insects, consider that hexapodous insects were not ordinarily differentiated until post-palæozoic time, and class all fossil insects before this time in a single order, termed Palæodictyoptera, since these fossils cannot be referable to any of our modern orders.

Most of these insects, however, show neuropterous and orthopterous affinities and demonstrate the great age of these insects. As we ascend the geological strata, insects become better differentiated and other orders appear—the Hemiptera, Coleoptera, etc., but no trace of hymenopterous insects appears until the tertiary formation is reached.

The earliest known fossil Hymenoptera occur in England in the middle Oölite, while in this country they have been obtained from different localities in the tertiary formation. Scudder in his Tertiary Insects of North America (U. S. Geol. Surv., 1890) describes 15 fossil terebrants and 8 aculeates from the Florissant beds of Colorado.

These fossils, however, are of so recent a date that, with one or two exceptions, all are referred to modern genera, and all belong to well-defined modern families, so that no clew as to the origin of the order is obtainable from geological strata and we must look to other sources for this information.

This clew, I believe, may be obtained, at least approximately, from living forms and from the position assigned the order by various systematic workers.

Position Assigned the Hymenoptera by Different Authorities.

The older authors divided insects into two principal groups: (1) The Mandibulata, or insects with jaws fitted for biting; and (2) The Haustellata, or insects with the mouth-parts fitted for sucking. From Westwood I find that Lamarck thought the Hymenoptera were the connecting order between the two series. Latreille placed it between the Neuroptera and the Lepidoptera, regarding Phryganea and Termes as forming the link between them, considering the long-tongue bees as approaching nearest to the Lepidoptera.

MacLeay, on the other hand, placed the Hymenoptera between the Coleoptera (with which they are supposed to be connected by the osculant order Strepsiptera) and the Trichoptera, the Tenthredinidæ being considered as trichopterous and the Uroceridæ as forming an osculant order, Bomboptera, between Trichoptera and Hymenoptera, which last order is reduced to the species possessing apodal larvæ: thus by means of the connection between the ants (Formicidæ) and white ants (Termitidæ), and the caddice-flies (Phryganeidæ) and the saw-flies (Tenthredinidæ), a strong relationship is shown to exist between the Linnæan orders Hymenoptera and Neuroptera.

Packard in his paper entitled On Synthetic Types in Insects (Bost. Journ. Nat. Hist., vii, p. 591–22, 1863) says that the Coleoptera, Hemiptera, Orthoptera, and Neuroptera "seem bound together by affinities such as those that unite by themselves the bees, moths, and flies," and to the latter or what he considers the higher series he has since applied the term Metabola, and to the former Heterometabola. He says: "The Metabola are unquestionably more homogeneous than the other group. One of their primary features is found in the more clearly marked regional divisions of the body; this is a consideration of great significance, since in the progress of structure, from the worms, through the crustaceans to the insects; or with the progress of structure, from myriapods, through the arachnids to the hexapods; or in the developmental history of the Metabola themselves, from the larva, through the pupa to the imago, we discover constantly increasing concentration of the segments of which the body is composed into distinct regions, culminating in the Hymenoptera, where head, thorax, and abdomen are most sharply defined."

All the orders of the Heterometabola and none of the Metabola are represented in the palæozoic rocks. Scudder states: "This is the more striking from the fact that if we omit mention of the single discovery of insect wings in the Devonian, the three orders of insects—hexapods, arachnids, and myriapods—appear simultaneously in the Carboniferous strata. The Metabola are then later in time and more perfect in development than the Heterometabola."

Packard also believes the Hymenoptera are descendant from the Lepidoptera.

Thus we see that most authorities are agreed as to the affinities existing between the Hymenoptera and Lepidoptera, and there is scarcely any doubt in my own mind now that this is the correct view, and that these two orders with the Trichoptera and part of the Diptera had a common ancestry.

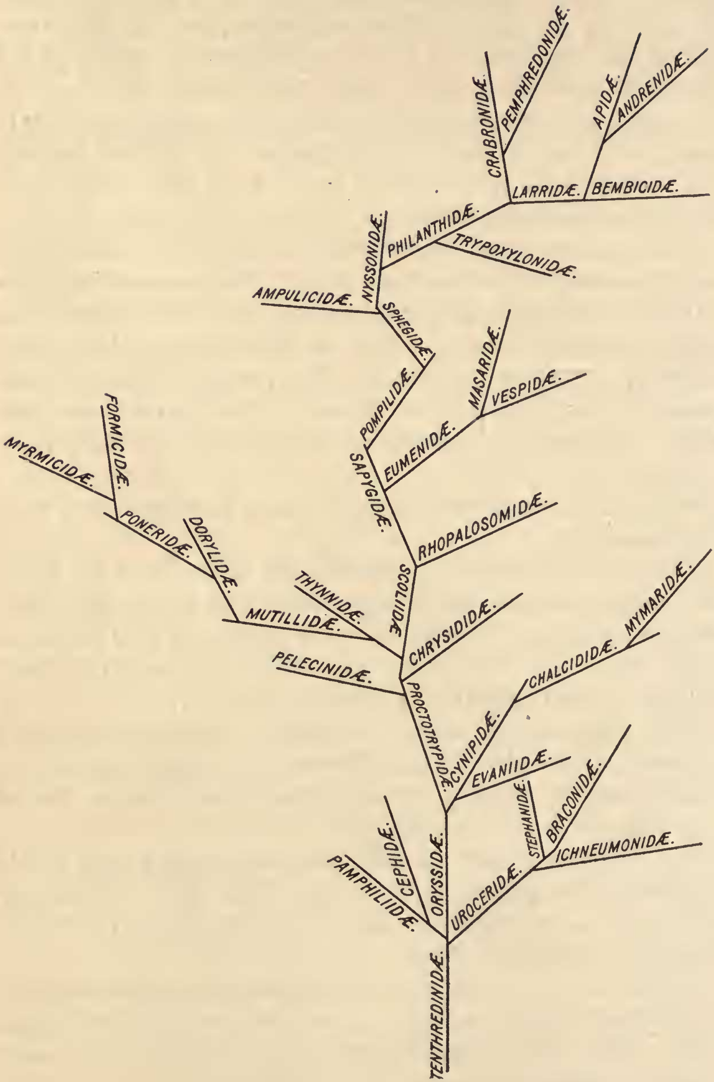
This relationship is shown in the close resemblance between the larvæ of the phytophagous Hymenoptera and those of certain lepidopterous larvæ, although the direct line of descent cannot be pointed out absolutely.

The relationship will probably be found among some of the wood-boring Lepidoptera, *Cossidæ*, *Ægeriidæ*, *Hepialidæ*, etc., and more particularly among those lepidopterous insects furnished with an ovipositor.

The larvæ of the Mecaptera (Panorpidæ) also approach close to the Hymenoptera, and the peculiar rostrate head of the imagoes of this order is frequently reproduced among the parasitic species (Agathis, Cremnops, etc.).

Mr. Nathan Banks has suggested that the Megaptera were the

DIAGRAM NO. 2.



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ancestors of the Diptera. There is apparently a close relationship between these insects and certain *Tipulidæ.*

In my diagram No. 2, I have attempted to show the development and relationship of the different families of the Hymenoptera, and to illustrate how the phytophagous species, whose larvæ are furnished with legs, in time gave place to higher and more specialized forms, whose larvæ are apodous.

I consider the Tenthredinidæ to be the lowest of hymenopterous insects, and from these in time were evolved on one hand the Cephidæ and Oryssidæ, on the other hand the Uroceridæ.

From the latter probably evolved the Braconidæ and Ichneumonidæ, in which the egg-boring apparatus is usually well developed. From the Oryssidæ were evidently evolved other forms, in which the egg-boring apparatus becomes variously modified and gradually develops into a true sting, and from which in time came the true aculeates—wasps, bees, etc. It is the stem of three or four different families.

The family Stephanidæ is evidently a branch of the Oryssidæ, with strong braconid affinities. The Cynipidæ, Proctotrypidæ, and Evaniidæ also had a common origin and in time evolved other forms.

From the Cynipidæ came the Chalcididæ, a recent type; while from the Proctotrypidæ, which I believe represent some of the most ancient types of hymenopters, we have a distinct line of descent into the Scoliidæ, Mutillidæ, and the higher Aculeata.

My diagram will sufficiently show my conception of the relationship of these families, and I will therefore close with a brief synopsis of a new classification of these insects, based upon their relationship as illustrated in my diagram.

I. Sub-order Heterophaga.* Abdomen petiolate or subpetiolate, never broadly sessile; larvæ apodous.

* Hypopygium entire and closely united with the pygium, the sting or ovipositor always issuing from tip of abdomen.

a. Pronotum not extending back to tegulæ.
Tarsi dilated or thickened.. I. Anthophila Hartig.
Tarsi slender, not dilated...II. Entomophila Ashm.

aa. Pronotum extending back to the tegulæ.

† Apical segments of abdomen normal.

° Petiole or first segment of abdomen simple, without scales or nodes.
Wings usually folded longitudinally in repose; if straight the antennæ ending in a large club.
III. Diplopteryga Latr.

Wings not folded longitudinally in repose............IV. Fossores Latr.

° Petiole or first segment of abdomen with one or more scales or nodes; sexes usually 3, ♂ ♀ ☿.........V. Heterogyna Latr.

†† Apical segments of abdomen tubular and retractile, telescopic-like, visible dorsal segments from 3–5...........VI. Tubulifera Latr.

††† Apical segments of abdomen usually tubular, but not retractile or telescopic-like.
VII. Oxyura Latr.

** Hypopygium divided or never united with the pygium; ovipositor originating some distance before tip of abdomen.
Front wings without a stigma...VIII. Stenospili Ashm.
Front wings with a stigma...... IX. Megaspili Ashm.

II. Sub-order Phytophaga.** Abdomen broadly sessile; larvæ with legs.
Anterior tibiæ with 1 apical spur..................... I. Xylophaga.
Anterior tibiæ with 2 apical spurs ....II. Phyllophaga.

The series indicated above represent the following families, which may be arranged consecutively thus:

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* Petioliventres Haliday. ** Sessiliventres Haliday.

Anthophila	I.	Apidæ.
	II.	Andrenidæ.
Entomophila	III.	Crabronidæ.
	IV.	Pemphredonidæ.
	V.	Bembicidæ.
	VI.	Larridæ.
	VII.	Trypoxylonidæ.
	VIII.	Philanthidæ.
	IX.	Nyssonidæ.
	X.	Sphecidæ.
	XI.	Ampulicidæ.
Diplopteryga	XII.	Masaridæ.
	XIII.	Vespidæ.
	XIV.	Eumenidæ.
Fossores	XV.	Pompilidæ.
	XVI.	Sapygidæ.
	XVII.	Rhopalosomidæ.
	XVIII.	Scoliidæ.
	XIX.	Thynnidæ.
	XX.	Mutillidæ.
Heterogyna	XXI.	Poneridæ.
	XXII.	Dorylidæ.
	XXIII.	Formicidæ.
	XXIV.	Myrmicidæ.
Tubulifera	XXV.	Chrysididæ.
Oxyura	XXVI.	Pelecinidæ.
	XXVII.	Proctotrypidæ.
Stenospili	XXVIII.	Cynipidæ.
	XXIX.	Chalcididæ.
	XXX.	Mymaridæ.
Megaspili	XXXI.	Evaniidæ.
	XXXII.	Trigonalidæ.
	XXXIII.	Stephanidæ.
	XXXIV.	Braconidæ.
	XXXV.	Ichneumonidæ.
	XXXVI.	Agriotypidæ.
Xylophaga	XXXVII.	Oryssidæ.
	XXXVIII.	Siricidæ.*
	XXXIX.	Cephidæ.
Phyllophaga	XL.	Pamphiliidæ.
	XLI.	Tenthredinidæ.

Tables defining the above families are already prepared and will be published in a separate paper. This arrangement is given now, in connection with the diagram, merely to show how these families are arranged in my collection, so as to exhibit their true relationship.

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* Uroceridæ of American authors.

You have now had a modern opinion as to the origin and development of the Hymenoptera, and, in conclusion, I shall bring my address to a close by a quotation from Cowan, as to the opinion held by the ancients, respecting the development of the bees and wasps:

He says: "It was the general opinion of antiquity that Bees were produced from putrid bodies of cattle. Varro says they are called *Βουγόναι* by the Greeks, because they arise from putrefied bullocks. In another place he mentions their arising from these putrid animals, and quotes the authority of Archelaus, who says Bees proceed from bullocks, and Wasps from horses.: Virgil, however, is much more satisfactory, for he gives us the recipe in all its details for producing these insects:

"First, in a place, by nature close, they build
A narrow flooring, gutter'd, wall'd, and til'd.
In this, four windows are contriv'd, that strike
To the four winds oppos'd, their beams oblique.
A steer of two years old they take, whose head
Now first with burnished horns begins to spread:
They stop his nostrils, while he strives in vain
To breathe free air, and struggles with his pain.
Knock'd down he dies: his bowels bruis'd within,
Betray no wound on his unbroken skin.
Extended thus, in his obscene abode,
They leave the beast; but first sweet flowers are strow'd;
Beneath his body, broken boughs, and thyme,
And pleasing Cassia, just renew'd in prime.
This must be done, ere spring makes equal day,
When western winds on curling waters play:
Ere painted meads produce their flowery crops,
Or swallows twitter on the chimney tops.
The tainted blood, in this close prison pent,
Begins to boil, and thro' the bones ferment.
Then wondrous to behold, new creatures rise,
A moving mass at first and short of thighs;
Till shooting out with legs, and imp'd with wings.
The grubs proceed to Bees with pointed stings:
And more and more affecting air, they try
Their tender pinions and begin to fly."
